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# THE USE OF MARKING DATA IN FISH POPULATION ANALYSIS

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# THE USE OF MARKING DATA IN FISH POPULATION ANALYSIS

by

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FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATIONS
Rome, June 1976

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M-43
ISBN 92-5-100051-4

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## PREPARATION OF THIS PAPER

This document is based on and updates Fisheries Technical Paper No. 51, Suppl. 1. It is one in a series of manuals and other documents prepared by the Fishery Resources and Environment Division to assist scientists at all levels concerned with marine research and its application to fisheries. It is concerned with one aspect of the use of tagging in marine research - that of the mathematical analysis of the results to provide estimates of quantities (population numbers, mortalities, growth and dispersion) useful in further analysis of fish populations. It is planned to produce further reports dealing with other aspects of tagging - including the general purposes of tagging work, its advantages and disadvantages - choice of tag; methods of capture and handling of fish; and methods of ensuring good reporting of recaptured fish.

Distribution

FAO Department of Fisheries
FAO Regional Fishery Officers
Selector SM
Selector SI
Author

Bibliographic entry

Jones, R. (1976)
FAO Fish.Tech.Pap., (153):42 p.
The use of marking data in fish population analysis

FAO manuals. Methodology. Marking. Tagging. Population studies. Migrations. Stock assessment. Survival. Mortality. Fishing mortality. Growth rate. Statistical analysis. Statistical tables.

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This paper deals with the mathematical treatment of tagging data for estimating survival rates, population size, growth rates and movement parameters. It revises and updates an earlier paper with the same objective (Jones, 1966).

## 1. Estimating Survival Rates

One of the objects of tagging experiments is to estimate the survival rate of the individuals in the tagged population. The final estimate may be expressed in terms of the proportion of individuals that survive for one year (S) or as an instantaneous coefficient of total mortality (Z), where

$$S = \exp(-Z).$$

There are a number of methods for estimating survival rates and these may be conveniently divided into two groups:

(a) Methods for estimating survival rate when tagging has been done on one occasion only.

(b) Methods for estimating survival rate when tagging has been done on more than one occasion.

### 1.1 Estimating survival rate from a single tagging experiment

If tagging is done on only one occasion, the survival rate has to be determined from the rate of decline of the tagged individuals.

Recaptures may be made in one of two ways. One method is to take samples from the population on a number of occasions and to record the numbers bearing tags in each sample. This method is appropriate if it is possible to tag so large a proportion of the population that the expectation of obtaining tagged fish within subsequent samples is reasonably high. When dealing with many commercial fish populations, however, the proportion of the total stock that can be tagged may be extremely small. As a result the expectation of obtaining tagged fish in subsequent samples is often also very small. In this situation, the experimenter may be dependent on commercial fishermen for the recapture of tagged individuals and, in this situation, the recaptures will be returned more or less continuously.

Whichever method of recapture is used it is implicit in the methods used that the numbers of recaptures can be expressed in units proportional to the total numbers of tagged individuals remaining in the population at successive times. There are various ways of doing this. To be precise, let

$n_i$ be the number of individuals taken in a sample on the ith occasion

$m_i$ be the number of these found to bear tags

$y_i$ be some function of $m_i$ that is assumed to be proportional to the number of tagged individuals in the population.

There are at least three possible choices of the function $y_i$. One is $y_i = m_i/n_i$, which requires the assumptions that the proportion of tagged individuals in the sample is the same as in the total population, and that the size of the population does not change during the experiment. A second choice is $y_i = m_i/f_i$, where $f_i$ is the fishing effort expended in collecting the ith sample. If the sampling effort is the same on every occasion, the simpler form $y_i = m_i$ may be chosen.

If the tagged individuals are recaptured continuously, then choices of $y_i$ can be made in the same way. Thus, values of $y_i$ may be calculated either from the ratio of numbers of

tagged individuals to total numbers of individuals caught over a period of time or they may be calculated from the number of tagged individuals taken per unit of fishing effort over some specified period of time, depending on the data that is available and the assumptions that are appropriate.

There are a number of methods of estimation based on the assumption that the survival rate is constant over the experimental period. Estimates of survival rate can then be obtained given successive values of $y_i$ taken either at equally spaced moments in time or over successive periods of equal duration.

Table 1 shows four methods of estimation that can be used for estimating the survival rate from a single tagging experiment when the recaptures are made on discrete occasions. The values in the row $m_i$ refer to number of individuals recaptured on six occasions. In the row $n_i$ are given the total numbers of individuals obtained on each sampling occasion. The values in the row $y_i$ have been calculated assuming that the proportion of tagged individuals in each sample is proportional to the number of tagged individuals in the sea. For convenience, these estimates have been multiplied by $10^4$. Thus, on the second occasion

$93 = (140 \times 10^4)/15\,000$.

Four methods of determining the annual survival rate are given. The first method is due to Jackson (1939) and was referred to by him as his "positive method". His estimate for the survival rate is

$$S = (y_2 + y_3 + \ldots\ldots y_k)/(y_1 + y_2 + \ldots\ldots y_{k-1}).$$

Jackson also refers to an alternative formula proposed by W.M. Stevens which is

$$S = [(y_3 + y_4 + \ldots\ldots y_k)/(y_1 + y_2 + \ldots\ldots y_{k-2})]^{\frac{1}{2}}.$$

Chapman and Robson (1960) thought that these estimates suffered from the disadvantage that they could take values greater than unity and considered that a better estimate of the survival rate was given by a modified estimate due to Heincke (1913) which is equivalent to

$$S = (y_2 + y_3 + \ldots\ldots y_k)/(y_1 + y_2 + \ldots\ldots y_k)$$

Robson and Chapman (1961) consider methods of analysing catch curves and their methods of estimating survival rate can be applied to data such as those in Table 1. The procedure is as follows.

First a total coded age (X) is calculated where

$X = \Sigma(i - 1)y_i$ for $i = 1, 2, \ldots J$ (the number of samples).

The second step is to calculate the mean coded age ($\bar{x}$) where

$$\bar{x} = X/\Sigma y_i.$$

The final step depends on the number of tags still outstanding after the last (Jth) sample has been collected. If, at the final sampling, it is supposed that the proportion of tagged individuals still at large is too large to be neglected then the estimate of mean coded age is equivalent to

$$\bar{x} = \sum_{i=1}^{J-1} i S^i / \sum_{i=0}^{J-1} S^i.$$

This equation cannot be solved directly for S but estimates of S needed to satisfy any given value of $\bar{x}$ can be determined for any value of J using Table 3 of Robson and Chapman (1961). Thus, for the example in Table 1, $\bar{x} = 1.5319$ and J = 6. From Robson and Chapman's Table 3 it can be seen that for 6 classes this value of $\bar{x}$ is satisfied by a value of S = 0.70. If sampling continues until the number of tagged individuals remaining in the sea is negligible then Robson and Chapman's method can be simplified. Suppose, for example, in Table 1 sampling had been continued on occasions 7, 8, 9, etc., until no further tagged individuals were obtained. Suppose also that the entry given for occasion 6 represents the total numbers obtained over the 6th and all subsequent occasions. In that case an estimate of survival rate is given directly by

$$S = X/(\Sigma y_i + X - y_6).$$

Using the data in Table 1, for example, this would have given

$$S = 553/(361 + 553 - 18)$$

$$= 0.62.$$

Table 2 illustrates the same methods of computation for the situation where values of $y_i$ have been obtained from the catch per unit effort of the tagged individuals on a number of occasions. Each value of $y_i$ is given simply by the ratio of the number caught and the fishing effort ($f_i$). Thus, for example,

$$9.66 = 140/14.5.$$

Table 3 shows similar calculations for the situation where individuals have been recaptured continuously over a period of 4 years. The periods have been coded from 1 to 4 and the numbers recaptured have been converted to numbers per unit effort to provide values of $y_i$. Estimates using the methods of Jackson, Stevens, Heincke, and Robson and Chapman can then be obtained exactly as before.

In addition to these methods, regression estimates can also be made. These are based on the fact that, given a constant mortality rate, the decline in the numbers of tagged individuals can be expected to approximate to an exponential curve. An exponential curve can be made linear with respect to time by taking logarithms of the numbers alive at equal intervals. A regression of log numbers against time should then provide an estimate of the instantaneous mortality coefficient, Z, directly. This method has been developed by Beverton and Holt (1956), Gulland (1969) and Paulik (1963).

Thus, suppose fishing effort is constant throughout the experiment and let $y_i$ be the number of tagged individuals recaptured during the ith period after tagging. Each period being of duration p (i.e., the ith period extends from time (i - 1)p to time ip), it follows that

$$y_i = FT(\exp(-Z(i-1)p))(1 - \exp(-Zp))/Z,$$

$$(i = 1, 2, 3 \ldots\ldots)$$

where F is the instantaneous mortality rate due to fishing
T is the number of tagged fish released
Z is the instantaneous mortality rate due to fishing and all other causes, including tagging mortality subsequent to the time of tagging.

This equation can be made linear with respect to i by taking logarithms of both sides. Thus

$$\log (y_i) = -Z (i - 1)p + \log (FT) + \log ((1 - \exp (-Z))/Z).$$

This shows that by plotting the natural logarithms of $y_i$ against the dummy variable i, a line of the slope -Zp is obtained (Beverton and Holt, 1956; Jones, 1956). An example is shown in Table 4. This shows, for comparative purposes, the same numbers of individuals captured per unit effort as were used in Table 3. Natural logarithms of these numbers have been calculated and a regression of $\log (y_i)$ on i is found to give

$$\log (y_i) = 5.347 - 0.430\ i$$

This equation shows that the estimate of Zp = 0.430. Since the grouping period is one year p = 1 and hence Z = 0.430 also. S is then obtained directly from the relationship

$S = \exp (-Z)$ so that

$S = 0.65$

This, it can be noted, is similar to values obtained using the methods of Jackson, Stevens, and Robson and Chapman.

Table 5 shows a similar example using the same basic data but with the regression method of Gulland (1969). This method differs from that of Beverton and Holt simply in that the coded periods are labelled 0.5, 1.5, etc., instead of 1, 2, 3, etc. This method of coding is to simplify the estimation of F which will be discussed later. Again, the regression of $\log (y_i)$ on i gives a slope of -0.430. Hence Zp = 0.430 and hence the estimate of S is 0.65 as was obtained in Table 4.

Table 6 shows the method described by Paulik (1963) based on the same principle but using a weighted regression technique. Paulik uses for weights, the values of $y_i/T$, where T is the number initially tagged. In Table 6, T is taken as 1 000. Instead of values of $\log (y_i)$ the regression is carried out using the logarithms of $y_i/T$. The numerical values are shown in the table and the weighted regression has a slope of -0.438. The estimate of S finally obtained is 0.645, similar to the value obtained by the previous methods.

Some of the methods have been described with reference to the situation in which recaptures have been made on discrete occasions, and others have been applied to situations where recaptures are made continuously. There seems no objection, in principle, why both methods of analysis should not be applied to both situations. The distinctions above relate more to the way in which these methods have been developed by different authors than to restrictions in the way in which they can be used.

Paulik (1963) compared the regression method shown in Table 6 with the maximum likelihood method described by Robson and Chapman. He considers the regression method to be more useful for general application since it requires only easy computations regardless of the number of recovery periods involved. However, in the situation where the numbers of individuals returned in some of the time periods are small or zero, the regression method would not necessarily be satisfactory and in this situation the maximum likelihood estimates of Robson and Chapman are to be preferred.

Another way of estimating a mortality rate from a single tagging experiment is described by Gulland (1955). He considers the situation in which the times from liberation to recapture are known for each fish recaptured and there are no tagged fish outstanding at the end of the experiment. He then assumes that the number of tagged fish declined exponentially with a constant mortality rate (Z) and shows that $\bar{t}$ is an unbiased estimate of $1/Z$ where $\bar{t}$ is the mean time of freedom of the recaptured individuals. To a first approximation therefore $1/\bar{t}$ is an estimate of Z. An example is shown in Table 7. The basic data are the actual

days of freedom of the individual recaptures. In the example these have a mean of 63 days which is equivalent to 0.17 years. The annual value of Z is therefore equal to 5.9.

Paulik (1963) considered maximum likelihood estimates for the Gulland model when some tags may still be outstanding and showed that an estimate of the annual survival rate (S) can be obtained from the following equation:

$$-1/\log (s^U) - s^U/(1 - s^U) = \bar{t}/U,$$

where U is the duration of the recovery period. Provided $\bar{t}$ is less than half of the total recovery period this equation can be solved with the aid of a table given by Deemer and Votaw (1955, p. 501, Table 1). An example is given in Table 7.

1.2 Estimating mortality from more than one tagging experiment

A considerable number of theoretical papers have been written on the analysis of multiple tagging and recapture experiments. By this is meant experiments in which individuals are tagged on more than one occasion and sampled for recaptures on more than one occasion. In experiments in which there is a relatively high probability of recapture, multiple tagging leads to the possibility of recapturing and releasing the same individuals on more than one occasion.

After the first sampling there may be individuals which have been recaptured on more than one occasion. If so, there are three ways of classifying the data:

(a) A recaptured individual can be classified with reference to all the occasions on which it has been previously tagged and released.

(b) A recaptured individual can be classified with reference only to the occasion on which it was first released.

(c) A recaptured individual can be classified with reference only to the occasion on which it was last released.

The first method has been considered by Jackson (1939, 1948) and Fisher and Ford (1947). Later workers have considered that this is a less efficient method than grouping individuals according to the occasion on which they were last released (Leslie and Chitty, 1951; Moran, 1952).

Figure 1 shows a general way of classifying the numbers returned. It is assumed that individuals have been tagged on sampling occasions 1 to 6. Recaptures have been made on sampling occasions 2 to 7. The numbers returned from each experiment and each sampling time are indicated by $m_{ij}$ (thus $m_{25}$ refers to individuals released on occasion 2 and recaptured on occasion 5). If grouping method No. 2 is used this would refer to individuals first released on sampling occasion 2. If grouping method 3 is used however, this would refer to individuals last released on occasion 2 (i.e., some of them could have been first released on occasion 1 but then recaptured and subsequently released on occasion 2).

The numbers released on any occasion have also been classed in different ways by different authors. One way is to count only the individuals that are newly tagged and released on each occasion. The other is to count the total number released on each occasion (i.e., individuals tagged for the first time plus any recaptures already bearing tags that are successfully released again).

1.2.1 The Jolly-Seber method

The most general solution is one proposed independently by both Jolly (1965) and Seber (1965). The model is stochastic and, according to Cormack (1969), the solutions

arrived at are so much simpler to apply than those obtained from the corresponding deterministic model that they should totally supersede them.

In the Jolly–Seber model recaptures are grouped according to the last time an individual is released (method "c" above). The numbers released are classified according to the total number released on each occasion (i.e., newly tagged + previously tagged). The situation is illustrated diagrammatically in Figure 2. Tagging and capturing are both done during brief periods, between which are longer periods in which no recaptures are made and no tags are released. Consider, for example, the situation at the beginning of the third tagging period. At that moment there will be $I_3'$ tagged individuals in the sea. During the duration of the third tagging period $m_3$ of these will be recaptured and successfully released again as part of the $T_3$ individuals released at the end of the third tagging period. This means that at the end of the third tagging period $T_3$ individuals will have been released and there will be $(I_3 - m_3)$ individuals in the sea bearing tags that were tagged prior to the beginning of the third period. It should be noted that $I_3$ will be smaller than $I'_3$ because of mortality of fish in the sea during the course of the tagging period. During the remainder of their lives $q_3$ out of these $(I_3 - m_3)$ individuals will be recaptured. Similarly $r_3$ out of the $T_3$ individuals will be recaptured. It follows then that by simple proportion

$$q_3/(I_3 - m_3) = r_3/T_3$$

hence $I_3 = m_3 + q_3 T_3/r_3$.

Similar considerations during the fourth experiment lead to the relationship

$$I_4 = m_4 + q_4 T_4/r_4.$$

The proportion surviving from the end of the third experiment to the beginning of the fourth experiment is then given by

$$S'_{3/4} = I'_4/(I_3 - m_3 + T_3).$$

Similarly, the proportion surviving from the end of the third experiment to the end of the fourth experiment is given by

$$S_{3/4} = I_4/(I_3 - m_3 + T_3)$$

so that

$$S_{3/4} = r_3(T_4 q_4 + r_4 m_4)/(r_4 T_3 (q_3 + r_3)).$$

In general it follows that the relationship for survival rate is given by

$$S_{t/t+1} = r_t(T_{t+1} q_{t+1} + r_{t+1} m_{t+1})/r_{t+1} T_t (q_t + r_t).$$

An example is given in Table 8 which shows the numbers tagged on four occasions and the numbers returned, classified according to the scheme in Figure 1. It is assumed that all individuals captured that already bear tags are released again. Thus, for example, of the 1 656 individuals tagged on occasion three, 156 of them were already bearing tags so that only 1 500 were freshly tagged. The first step in the calculation was to calculate the column totals $(m_i)$ and the row totals $(r_i)$. The next step was to calculate values of q noting that $q_1 = 0$ in all cases. Values of S were calculated using the formula above.

1.2.2 Robson's method

An alternative solution to the Jolly-Seber method is one proposed by Robson (1963). In this method the recaptures and the numbers tagged are classed in a different way from that used in the Jolly-Seber model. They are classed according to the occasion on which they were last released and the number tagged on each occasion refers only to the number newly tagged. It does not include any individuals that happen to be recaptured bearing tags and released again. The situation is illustrated diagrammatically in Figure 3.

Consider, for example, the situation at the end of the third tagging occasion. At that moment there will be $I_3$ tagged individuals in the sea. Of these $q_3$ will be captured subsequently. At the same time, $T_3$ individuals will be tagged and of these $r_4$ will be captured subsequently. It follows by simple proportion that

$$q_3/I_3 = r_3/T_3.$$

Similarly for the fourth experiment it follows that

$$q_4/I_4 = r_4/T_4.$$

The proportion surviving from the end of the third to the end of the fourth experiment is then given by

$$S_{3/4} = I_4/(I_3 + T_3)$$

$$= T_4\, q_4\, r_3/(T_3\, r_4\, (q_3 + r_3)).$$

A general formula then follows directly from this:

$$S_{t/t+1} = T_{t+1}\, q_{t+1}\, r_t/T_t\, r_{t+1}(q_r + r_t).$$

An example of the method is given in Table 9. It is assumed that the recaptures have been taken during discrete intervals at the tagging times. Note that $q_1 = 0$ and that other values of q are calculated as indicated in Figure 3. The estimates of the survival rate have been made using the formula above.

It should be noted that Robson's formula also lends itself to the situation in which the recaptures are made continuously and independently of the times when tagged fish happen to be released.

Robson's formula is equivalent to that of Jolly and Seber if the terms $m_i$ happen to equal zero. This would be so if the probability of recapturing a tagged individual during the course of tagging happened to be zero, as is liable to be the case when dealing with large populations.

An example is given in Table 10. It is assumed that the recaptures are made continuously, and that these have been grouped into periods corresponding with the periods in between each tagging experiment.

1.2.3 The triple catch method

This is a special case, dealing with the multiple tagging and recapture situation when there is sampling on three occasions only. On the first two occasions individuals are tagged; on the second and third occasions recaptures are recorded. There are two solutions depending on the method of grouping adopted.

Bailey (1951) grouped the recaptures according to the time of first marking. He obtained maximum likelihood estimates of survival rate from the end of the first sampling to the end of the second sampling occasion. His equation is

$$S_{1/2} = T_2\, m_{13}/(T_1\, m_{23}).$$

In this situation $m_{13}$ is equivalent to Robson's $q_2$. Also $m_{23}$ is equivalent to Robson's $r_2$. The result is equivalent therefore to Robson's result when i = 1 (note that $q_1 = 0$). An example is given in Table 11, based on data taken from Table 9. The same value of 0.60 is obtained for $S_{1/2}$ using Bailey's equation as was obtained using Robson's general equation.

The triple catch method was also considered by Leslie and Chitty (1951). They grouped recaptures according to the interval when they were last released and the estimate for survival rate from the end of the first sampling occasion to the beginning of the second is given by

$$S_{1/2} = (T_2\, m_{13} + m_3\, m_{12})/(T_1\, m_{23}).$$

This result is equivalent to Jolly and Seber's in the situation where i = 1, provided all of the individuals recaptured on the second occasion are returned unharmed to the population. An example is given in Table 12, using data from Table 8. The same value of 0.59 for $S_{1/2}$ is obtained using Leslie and Chitty's equation as was obtained by Jolly and Seber's general equation.

## 1.3 The estimation of fishing mortality from tagging experiments

Tagging experiments not only enable estimates to be made of annual mortality rates but, in principle at least, also enable these estimates to be split into components due to fishing mortality and due to other causes.

In the situation where only one tagging has been done, the regression methods of Beverton and Holt, Gulland and Paulik all provide estimates of F, the instantaneous rate of mortality due to fishing. In the case of the Beverton and Holt regression, the estimate of F is given by

$$F = Z(\exp(I_o - Zp))/(T(1 - \exp(-Zp)))$$

where $I_o$ is the intercept.

For the Gulland method the estimate is

$$F = (\exp(I_o))/(Tp).$$

For the method described by Paulik the estimate is

$$F = Z\,(\exp(I_o - Zp))/(1 - \exp(-Zp)).$$

Examples are given in Tables 13–15 using data from Tables 4–7. For all the examples a value is required for the initial number tagged and this has been assumed to be 1 000 individuals in all cases. Table 13 shows the application of the Beverton and Holt, and Paulik methods to the data from Tables 4 and 6. From Table 4 the intercept $I_o = 5.347$. The value 0.17 of F then follows from the formula. From Table 6 the intercept is -1.539; substitution of this in the appropriate equation also gives a value of F = 0.17. (It should be noted that the difference between two intercepts is that in the weighted regression the numbers recaptured were all divided by 1 000. Apart from statistical variations in the fitted

regressions, the differences between the two intercepts is therefore equivalent to the natural logarithm of 1 000 which is 6.99.)

An estimate of mortality rate can also be made in the case of those experiments in which the exact liberation times for each individual are known. The Gulland (1955) formula for estimating F is

$$F = m/(T\bar{t})$$

where m is the total number recaptured.

Chapman (1961) showed that for this model no minimum variance unbiased estimate of F exists but that the following estimate of F is almost unbiased:

$$F = (m - 1)/(T\bar{t}).$$

An example is shown in Table 15 using data from Table 7 and assuming that the number of fish tagged in the first instance was 1 000 individuals. In this example the values of F obtained using the Gulland and the Chapman formulae are both equal to 0.12.

An estimate of X which is equivalent to the mortality rate due to all causes other than fishing is equal to Z - F. In the example in Table 15 this is equal to 5.9 - 0.12 = 5.78.

When dealing with multiple tagging experiments there are two alternatives to consider. Tables 8 and 9 deal with the situation in which sampling for recaptures is done on the same occasions in which fish are captured for tagging. In this situation the rate of capture on the ith occasion ($p_i$) is given by

$$p_i = m_i/I_i'.$$

To a first approximation $I_i' = I_i$ provided the duration of each tagging experiment is negligible in relation to the total time in which tagged fish are tagged and recaptured. An estimate of $p_i$ is then given by $m_i/I_i$. Examples are given in Tables 16A and B using data from the examples in Tables 8 and 9. Estimates of $I_i$ have been taken from the basic formulae developed in Figures 2 and 3.

Estimates of fishing mortality F (as distinguished from the rate of capture $p_i$ above) can also be made in the case of multiple tagging experiments. Table 17, for example, illustrates a way of doing this using the data from Table 10. In this example it has been assumed that the recaptures have been made continuously during the periods between tagging experiments. Thus, for any one period it is possible to write

$$m = F N (1-S)/Z$$

where m is the number caught and N is the number of tagged individuals in the sea at the beginning of a recapture period (and hence at the end of a tagging period). Estimates of N at the end of any recapture period are equivalent to $T_i + I_i$ (see Figure 3) and this is given by

$$N = T_i + I_i = T_i (q_i + r_i)/r_i.$$

Given estimates of $N_i$, $m_i$ and $Z_i$, it is a simple matter to determine the values of F. Details are given in Table 17. Basic data have been taken from Table 10. The values of $N_i$ have been calculated using the formula above. Values of $Z_i$ have been calculated from the relationship

$$Z = -\log (S).$$

Estimates of F have then been obtained from the relationship

$$F = Z\, m/N(1-S).$$

1.4 Some factors that can influence the estimates of survival rate obtained from tagging experiments

There are a number of systematic errors that can influence tagging estimates and these have been classes as types A, B and C by Ricker (1958). The underlying assumption of all methods of analysis is that in the constant parameter situation the numbers of tagged fish will tend to decline exponentially with time. This means that the logarithm of the numbers alive at any moment should be linearly related to time as shown by the continuous lines in the diagrams in Figure 4. By type A errors are meant those errors that tend to influence the intercept but not the slope of the regression. This, for example, can happen if there is an initial mortality of tagged fish due to the act of tagging itself so that the number of live individuals liberated is smaller than the number actually tagged in the first instance. Type A errors can also occur if there is incomplete reporting of tags. In particular, if a constant proportion of the individuals recaptured are reported the effect will be to move the regression lines down, influencing the intercept but not necessarily the slope. If the slope of the regression is not affected, estimates of survival rate and total instantaneous mortality rate (Z) are not affected. The effect of an underestimate of the intercept, however, is to underestimate estimates of fishing mortality rate (F).

Errors of types B and C tend to influence the slope of the regression but not necessarily the intercept. The situation is illustrated diagrammatically in Figure 4. Type B errors occur if the act of marking causes marked fish to die at a greater rate than unmarked fish throughout the entire course of the experiment. They could also occur if there was progressive loss of interest in the experiment by fishermen so that the proportion of tags returned tended to decline during the experiment. Type C errors are those that cause the slope of the regression to be too great due to an emigration of marked fish from the experimental area.

The effect of errors of types B and C is to underestimate the survival rate and overestimate the total instantaneous mortality rate (Z). Errors of types B and C do not necessarily affect estimates of fishing mortality rate, however, providing they are made from the formulae of Gulland and Chapman which are not dependent on the estimates of Z.

2. The Determination of Population Size from Marking Experiments

Marking experiments can be used for determining the size of fish populations. In principle the methods are extremely simple and are based on some variation on a method of estimation known as the Petersen method.

2.1 The Petersen method

The Petersen method consists of tagging individuals on one occasion and sampling for recaptures on a single subsequent occasion. Suppose, for example, that there is a population of N fish and that T of these are tagged. The simplest situation is when the tagged fish are distributed at random throughout the population, or when the sampling effort is distributed at random. If the proportion of tagged fish in a sample should be the same as the proportion of tagged fish in the population, i.e., if there are m tagged fish in a sample of size n, then

$$\frac{m}{n} \text{ is expected to equal } \frac{T}{N},$$

so that on rearranging terms one gets

$$N = \frac{nT}{m}.$$

In the literature, the estimation formula does not always appear in this simple form because it is biased and needs to be corrected. The cause of the bias is that m, the number of marked fish in a sample of size n, is a random variable. Over many samples, the observed values of m/n will indeed average T/N, but it does not follow that the observed values of the reciprocal n/m, which is what appears in the estimation formula, will average N/T. Instead, their average will exceed N/T because, in technical terms, the expectation of the reciprocal always exceeds the reciprocal of the expectation. The simple formula, therefore, consistently overestimates population size.

A number of modifications of the basic equation are given in the literature to correct this bias. These are summarized in Table 18. Equations (A) - (C) are used when the sampling is "direct"; i.e., sampling until a sample size (n) has been obtained. (The sample size may be predetermined but there is no theoretical requirement to fix n before sampling starts, and in practice it is usually impossible to control sample size anyway.) An alternative procedure, known as "inverse" sampling, is to continue sampling until a predetermined number of tagged animals (m) has been recovered. The appropriate equation for this situation is given in (D) of Table 18.

Examples of population estimation using the Petersen method are given by Ricker (1958), Hancock (1963), Le Cren and Kipling (1963), Sato (1938) and Simpson (1963).

The reason for the extreme simplicity of the Petersen method lies in the assumptions on which it is based. The fact that either the fish or the sampling effort should be randomly distributed has already been referred to. Another important assumption is that the tagged and untagged fish are equally liable to capture and, if this does not hold, population estimates are likely to be biased (Carlander and Lewis, 1948; Junge, 1963). Anderson and Bagge (1963) describe how plaice tagged with Petersen discs were caught up in the material of meshes through which they would otherwise have escaped. Their chances of capture were thereby increased; to estimate the increase further experiments had to be conducted using a different type of tag.

### 2.1.1 The number of fish that have to be tagged

The numbers of fish that have to be tagged and the size of the sample that has to be subsequently taken are directly related to the size of the population.

According to Robson and Regier (1964), to be sure of getting an unbiased estimate, it is necessary to take a sample large enough to be certain of recapturing at least one tagged fish; i.e., if T fish are tagged out of a population of N fish, then the subsequent sample (n) should be not less than N-T. They show that if this condition is not met the resultant estimate of N will be biased by approximately 100 exp $(-(T + 1)(n + 1)/N)$ percent. In order to ensure a negligible bias, Robson and Regier recommend that the product of T x n should exceed the population size (N) by a factor of at least 3 or 4. Robson and Regier give graphs for estimating how many fish should be tagged and how many fish should be sampled subsequently in order to estimate population size with various degrees of precision.

According to Cormack (1969) the distribution of nT/m is far from symmetrical, so that confidence limits cannot be set to the estimate of population size in the normal way. As a way out of this difficulty he suggests that confidence limits should be set to m/nT, since the distribution of this is more likely to be symmetrical. The reciprocals of these limits should then provide confidence limits that are less biased.

Davis (1964) gives graphs for setting confidence limits directly to population size for different values of population size, number tagged and number subsequently sampled.

## 2.2 Other methods

In practice it may not be possible to take a sub-sample of the population just after tagging. The longer the interval that elapses, however, the smaller is the likelihood that Petersen's equation in its simple form will still be applicable.

The assumption that $\frac{T}{N}$ is constant throughout the period in which recaptures are made is implicit in the Petersen equation. Ideally therefore, the Petersen method should be used before any mortality of tagged or untagged fish has had time to occur. The method is not necessarily restricted in this way, however, provided the mortality and/or emigration rate of tagged and untagged fish is the same. For example, suppose that after a certain period only a proportion, p, of the original population of N individuals remains alive within the sampling area. The losses may be due to mortality or emigration from the sampling area or to both. The population size is then Np. Provided the proportion of tagged fish that remains is also p, it follows that the ratio of tagged to untagged fish will be $\frac{Tp}{Np}$ which is still equivalent to $\frac{T}{N}$. If this is so, the basic equation could still be valid for estimating population size, even though tagged fish may have been recaptured over a considerable period of time, e.g., when tagged fish are recaptured by commercial fishermen over a period of several years.

If the recapture of tagged fish occurs over a long enough period, some account must be taken of changes in population size due to recruitment or immigration. If this happens, N, but not T, may actually increase so that the ratio $\frac{T}{N}$ will then no longer be constant. Instead it will decrease. The simplest situation is one in which the recruits, or immigrants, can be distinguished by their size or some other feature, from the original population. If that is so, they may be excluded from the sample of n individuals and then the basic Petersen method can still be applied.

If recruits or immigrants cannot be excluded, an alternative procedure due to Parker (1955) may be adopted. This method is based on the assumption that a decline in the proportion of tagged fish in the population will be reflected in a decline in the proportion of tagged fish in the samples; i.e., if $\frac{T}{N}$ declines, so also will $\frac{m}{n}$, where T is the number of tagged individuals in the population subsequent to tagging. Parker's method then consists of plotting the ratio $\frac{m}{n}$ against time. A line drawn through these points will have a negative slope, and if it is extrapolated back to zero time it will have an intercept that represents the value of $\frac{m}{n}$ at the time of tagging. This, of course, will represent $\frac{m}{n}$ before any recruitment or immigration has had time to occur and so will be the value of use in the Petersen equation. This method has been used by Hancock (1963) for estimating the size of whelk populations.

In a later paper Parker (1963) describes a method of estimating the rate of recruitment by using a model in which the rate of recruitment is assumed constant throughout the experiment. A system of equations is derived for estimating the population size, the rate of mortality and the rate of recruitment. These cannot be solved algebraically but a solution can be obtained by using the appropriate numerical technique.

Jolly and Seber give an estimate for population size which is identical to the Petersen equation; i.e.

$$N_i = n_i I_i / m_i .$$

The importance of the Jolly-Seber method, however, is that an equation is also derived for estimating the number of tagged individuals in the sea at the time of the ith sampling; i.e., they show that

$$I_i = m_i + q_i T_i / r_i$$

so that by substitution

$$N_i = (n_i\ q_i\ T_i / m_i\ r_i) + n_i.$$

An example is given in Table 19, using data from Table 16A, as well as a set of values of $n_i$ provided for the purpose of the example. Since values of $I_i$ have already been calculated, the estimates of population size follow directly from the Petersen equation in its simplest form. Note that $I_i$ is here assumed equal to $I_i'$. Similar estimates can also be obtained using values of $I_i''$ obtained by Robson's method (Table 16B). Estimates of $N_i$ then follow directly from the equation above.

Schnabel (1938) considered an extension of the basic Petersen equation in the special situation where there is no mortality or recruitment to the population. The method is a simple extension of the Petersen method to a series of samplings for tagging and recapture. Schnabel gives the following maximum likelihood equation for estimating the population size N.

$$\sum \left[ \frac{(n_i - m_i) I_i}{N - I_i} \right] = \Sigma m_i$$

It is assumed that $n_i/N$ is sufficiently small to ignore the complications of sampling without replacement (say, less than 0.1 according to Seber (1973)).

This equation can be solved for N, the population size by numerical methods (Seber, 1973; De Lury, 1951). An algebraic solution is possible too if various assumptions are made. Schnabel considered in particular the case where the number of tagged fish in the sea at the time of the ith sampling happens to be negligible compared with the population size N. If this is so, the equation can be simplified to give the following estimate of N:

$$N = \frac{\Sigma n_i\ I_i}{\Sigma\ m_i}.$$

Chapman (1952) suggested that a better estimate would be

$$N = \frac{\Sigma n_i\ I_i}{\Sigma m_i + 1}$$

whilst Schumacher and Eschmeyer (1943) suggested that more weight should be given to the numbers recaptured from large markings than from small by writing

$$N = \frac{\Sigma n_i\ I_i^2}{\Sigma m_i\ I_i}.$$

It has already been noted that these methods are based on the assumption of zero recruitment and mortality, and these are conditions that may only rarely be valid in practice.

In the case of the "Triple Catch" method, Bailey also derived estimates of $N_2$, the size of the population on the second tagging occasion, and $R_2$, the proportionate increase in the population between the second and third occasions due to recruitment and/or immigration. These estimates are:

$$N_2 = T_2\ n_2\ m_{13} / m_{12}\ m_{23}$$

$$R_2 = n_3\ m_{12} / n_2\ m_{13}$$

## 3. Estimating Growth from Marking Experiments

Marking results can provide valuable data for measuring growth, providing the marking process does not interfere with growth. This can be especially important for those species that cannot be aged or that can only be aged with difficulty.

### 3.1 Fitting a growth curve to data representing equal time intervals

The basic requirements are, first to construct an age/length or age/weight curve, and second to determine the parameters of a curve that fits the data well. For the second purpose, the von Bertalanffy curve is now widely used (von Bertalanffy, 1938, 1949) and details and examples of methods of fitting this curve are given by Gulland (1969).

### 3.2 Fitting a growth curve to data representing unequal time intervals

The methods described by Gulland (1969) are suited to the estimation of von Bertalanffy's growth parameters from growth data collected over equal time intervals. The growth increments of marked fish, however, extend over varying lengths of time and some modification of the usual method is required to deal with these data. A way of doing this has been described by Gulland and Holt (1959).

The basic von Bertalanffy equation is

$$l_t = L_\infty(1 - e^{-K(t - t_o)})$$

where $l_t$ = the length at age t and $L_\infty$, K and $t_o$ are the growth parameters. After some time interval a, the age will be t + a and the length will be

$$l_{t+a} = L_\infty (1 - e^{-K(t + a - t_o)}).$$

The growth increment can then be expressed by

$$l_{t+a} - l_t = L_\infty e^{-K(t - t_o)}(1 - e^{-Ka}).$$

Since the increments of marked fish will have occurred over varying time intervals they can be standardized to a first approximation by expressing them in terms of increments per unit time. What is required is a quantity

$$y = (l_{t+a} - l_t)/a$$

This is equal to

$$L_\infty e^{-K(t - t_o)} \left(\frac{1 - e^{-Ka}}{a}\right).$$

The next step is to relate this quantity to the average length during the growing period, i.e., to the length $\frac{l_{t+a} + l_t}{2}$. If this is called x,

$$x = L_\infty \left[1 - \tfrac{1}{2} e^{-K(t - t_o)} (1 + e^{-Ka})\right].$$

Rearranging terms gives

$$L_\infty e^{-K(t - t_o)} = \frac{2(L_\infty - x)}{1 + e^{-Ka}}.$$

Next, substituting the expression for y above, gives

$$y = (L_\infty - x)\frac{2(1 - e^{-Ka})}{a(1 + e^{-Ka})}.$$

Finally, putting $\frac{1}{2}Ka = b$ gives

$$y = K(L_\infty - x)\frac{\tanh b}{b}$$

where $\tanh b = (\frac{1 - e^{-2b}}{1 + e^{-2b}})$

or, alternatively

$$y\frac{b}{\tanh b} = K L_\infty - K x$$

From this equation it is clear that if $y\frac{b}{\tanh b}$ can be plotted against x, the result should be a straight line with a slope of -K and an intercept of $K L_\infty$.

An example is given in Table 20. The data in the first three columns are the recapture details for five fish. The values of y, the increment per unit time, and x, the mid point of each growing period, are calculated as shown. The next step is to plot y against x. The points will be found to lie on a straight line with a slope of -0.2. The first estimate of K which can be called $K_1$ is therefore 0.2. Using this value for K, $b_1$ can be calculated for each fish and the values of $\frac{b_1}{\tanh b_1}$ can be calculated or looked up in the table given by Gulland and Holt (1959). In the last column of Table 19 are shown the values of $\frac{y\, b_1}{\tanh b_1}$ for each fish.

In this example, the values of $\frac{b_1}{\tanh b_1}$ are so close to unity that the values in the last column of Table 19 are effectively the same as those of y. If they had not been the same, the procedure would have been to plot $\frac{y\, b_1}{\tanh b_1}$ against x to obtain a new line with a new slope. The slope of this line would have given a second estimate of $K(K_2)$ and the whole process could then have been repeated until the estimates of K remained unchanged. In practice, it should be noted that for values of b up to about 0.4, the values of $\frac{b}{\tanh b}$ remain close to unity so that a value of K can usually be obtained, as in this example, directly from the first plot of y against x.

When y is plotted against x using the above data, the line is seen to cut the x axis at a length of 90 cm. In other words, at a length of 90 cm the growth increment is zero, so that 90 cm is the required estimate of $L_\infty$.

The parameter $t_o$ cannot be estimated from the data given in Table 19 alone. It is also necessary to know the age of the fish at each of the 10 lengths recorded. If this is known, 10 values of $t_o$ may be determined, one from each length, and the values averaged to give a single value of $t_o$. Details are given by Gulland (1969).

## 4. The Determination of Movement Parameters from Marking Experiments

The simplest way of demonstrating the pattern of movement of a group of recaptured marked fish is pictorially. The position of recapture of each fish can be plotted on a chart in relation to its position of liberation and its mean direction and distance of travel can be indicated. The number of days at liberty can be indicated too against each recapture position if desired.

To do this for each fish individually is quite straightforward but there remains the problem of how to combine the values from individual fish so as to estimate the mean direction and velocity of travel as well as a coefficient of dispersion. The values required are:

$\psi$ the mean direction of movement

V the mean velocity in this direction

$a^2$ the mean square dispersion coefficient (Skellam 1951).

### 4.1 Direction of movement ($\psi$)

A way of determining the mean direction of movement can best be appreciated from Figure 5. Consider the case of a single fish that has been liberated at the centre of some conveniently chosen set of coordinates (A) and that is subsequently recaptured at position B. The position of recapture can be represented within the coordinate system by giving it a displacement r and a direction $\theta$. This method of representation is convenient in practice since r and $\theta$ are both values that can be meaningfully assigned to any recapture position.

For any one fish this method of representation is excellent but for more than one it is useful to transform to cartesian coordinates. If the axes of the reference system are labelled x and y it is easily seen that the displacement of a recaptured fish from the origin becomes

$r \sin \theta$ along the x axis, and

$r \cos \theta$ along the y axis

That this is so can be demonstrated from the right angled triangle (ABC) in Figure 6. Since

$$\frac{x}{r} = \sin \theta$$

it follows that $x = r \sin \theta$. Similarly,

$$\frac{y}{r} = \cos \theta$$

and therefore $y = r \cos \theta$. If there is more than one fish their total displacement along the x axis becomes

$$r_1 \sin \theta_1 + r_2 \sin \theta_2 + \ldots\ldots\ldots = \sum_i r_i \sin \theta_i$$

Similarly, the total displacement along the y axis will be given by $\sum_i r_i \cos \theta_i$.

These two displacements, $\Sigma r \sin \theta$ and $\Sigma r \cos \theta$ can be used to locate what is effectively the net displacement of the group as a whole. This is done by choosing a point B such that the values of x and y (the coordinates of B) are given by $x = \Sigma r \sin \theta$ and $y = \Sigma r \cos \theta$ (see Figure 7). Then, let R be the overall group displacement AB and let its component of direction be given by the angle $\psi$ (Figure 7).

It follows that since

$$\frac{x}{y} = \tan \psi$$

$$\tan \psi = \frac{\Sigma r \sin \theta}{\Sigma r \cos \theta}$$

An example is given in Table 21, wherein

$\Sigma r \sin \theta = 1.23$

$\Sigma r \cos \theta = -26.33$

$$\tan \psi = \frac{1.23}{-26.33} = -0.0467.$$

A tangent of +0.0467 indicates an angle of 2.7°. Therefore

$\psi = 180 - 2.7 = 177.3°$.

(Note: Since $\Sigma r \sin \theta$ is positive and $\Sigma r \cos \theta$ is negative it follows that $\psi$ lies in the quadrant from 90° to 180°.)

## 4.2 Mean velocity (V)

In Figure 7 the overall displacement of the group as a whole is denoted by R. Now, the total time that will have elapsed will be the sum of the periods of liberty of the individual fish. If these are $t_1$, $t_2$, etc., the total time of liberty can be denoted by $\Sigma t$. It follows then that an estimate of V, the displacement velocity of the group as a whole is given by $\frac{R}{\Sigma t}$; that is, by

$$V = \frac{\sqrt{(\Sigma r \sin \theta)^2 + (\Sigma r \cos \theta)^2}}{\Sigma t}.$$

Example: Determine a value of V from the data in Table 21

$$V = \frac{\sqrt{(1.23)^2 + (-26.33)^2}}{153} = \sqrt{\frac{694.8}{153}}$$

$= 0.17$ km/day

## 4.3 Mean square dispersion coefficient ($a^2$)

There is one more coefficient that is needed in order to describe the distribution of recaptures more fully. That is, a parameter is needed to measure, in some way, the extent to which individual fish move independently of one another. A high value of V and a low value of $a^2$, for instance, would signify a real directional movement with a low rate of dispersion about the group mean. A low value of V and a high value of $a^2$ would be suggestive of random movement with comparatively little directional movement.

As a basis for the estimation of a suitable dispersion coefficient the theoretical treatment by Skellam (1951) and Beverton and Holt (1957) of the physical theory of heat conduction has been employed. Details of the theory have already been published for the situation where the direction of movement ($\psi$) is known beforehand (Jones, 1959). It is only necessary here to refer to the result obtained there and then to consider its extension to the case where $\psi$ is unknown.

In the case where $\gamma$ is known

$$a^2 = \frac{1}{n}\left\{\sum \frac{r^2}{t} - \frac{(\Sigma r \cos \theta)^2}{\Sigma t}\right\}$$

In this formula it is assumed that each value of $\theta$ is measured from the actual direction of movement. Since in practice, it is convenient to measure $\theta$ from some direction such as true north, it is $(\theta - \gamma)$ rather than $\theta$ that should be used in the equation above; i.e., if $\theta$ refers to the displacement from true north then $(\theta - \gamma)$ refers to the displacement from the actual direction of movement. Thus,

$$a^2 = \frac{1}{n}\left\{\sum \frac{r^2}{t} - \frac{[\Sigma r \cos (\theta - \gamma)]^2}{\Sigma t}\right\}$$

Since $\gamma$ may be unknown it is desirable to eliminate $\gamma$ from the equation. If this is done, (Jones, 1966) the equation for $a^2$ simplifies to:

$$a^2 = \frac{1}{n}\left\{\sum \frac{r^2}{t} - \frac{(\Sigma r \cos \theta)^2 + (\Sigma r \sin \theta)^2}{\Sigma t}\right\}$$

$$= \frac{1}{n}\left\{\sum \frac{r^2}{t} - v^2 \Sigma t\right\}.$$

Example: Determine a value of $a^2$ from the data in Table 21

$$a^2 = \frac{1}{4}\left\{76.4 - \frac{694.8}{153}\right\}$$

$$= 18 \text{ km}^2/\text{day}$$

4.3.1 Significance of $a^2$

The mean square coefficient of dispersion ($a^2$) is really a compound parameter resulting from the product of $\varepsilon$, the mean distance travelled by each fish between each change of direction and v, the average swimming speed of each fish. That is,

$$a^2 = \varepsilon.v \text{ or } \varepsilon.\frac{\varepsilon}{w} = \frac{\varepsilon^2}{w}$$

where w is the mean time required to swim a distance $\varepsilon$. The fact that the numerator is the square of a distance explains why $a^2$ is expressed in units such as $\text{km}^2$/day. The fact that it is a compound parameter results from the fact that a given rate of dispersion could arise because the fish swim slowly with infrequent changes of direction or rapidly with frequent changes. Without further information it is not possible to discriminate between these alternatives.

A numerical value of $a^2$ such as 4 $\text{km}^2$/day can be employed in the following ways. First if $4.0 = a^2 = \varepsilon.v$, a table of $\varepsilon$ and v can be made up to satisfy this relationship. This is done in Table 22. If an upper limit can be set to the likely mean swimming speed v, then a lower limit is automatically set to the value of $\varepsilon$.

Second, a numerical value of $a^2$ can be substituted in the following equation to determine the proportion of fish expected to lie within a given distance of the marking position after a given time. The equation is

$$P(R, t) = 1 - \exp\left(-\frac{R^2}{a^2 t}\right)$$

where P (R, t) signifies the proportion of fish lying within a circle of radius R, after time t.

More generally, the equation

$$P(R_1, R_2, t) = \exp\left(-\frac{R_1^2}{a^2 t}\right) - \exp\left(-\frac{R_2^2}{a^2 t}\right)$$

can be used to determine the proportion of fish lying between two circles with radii $R_1$ and $R_2$ respectively.

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Table 1

Estimation of survival rate from a single tagging experiment with recaptures on discrete occasions - I

| i | 1 | 2 | 3 | 4 | 5 | 6 |
|---|---|---|---|---|---|---|
| $m_i$ | 120 | 140 | 16 | 35 | 40 | 29 |
| $n_i$ | 10 000 | 15 000 | 3 000 | 8 000 | 12 000 | 16 000 |
| $y_i$ | 120 | 93 | 53 | 44 | 33 | 18 |

**Jackson**

$$S = (93 + 53 + 44 + 33 + 18)/(120 + 93 + 53 + 44 + 33)$$
$$= 0.70$$

**Stevens**

$$S = [(53 + 44 + 33 + 18)/(120 + 93 + 53 + 44)]^{\frac{1}{2}}$$
$$= 0.69$$

**Heincke**

$$S = (93 + 53 + 44 + 33 + 18)/(120 + 93 + 53 + 44 + 33 + 18)$$
$$= 0.67$$

**Robson and Chapman**

$$\Sigma_i(i - 1)y_i = 93(1) + 53(2) + 44(3) + 33(4) + 18(5) = 553$$

$$\Sigma y_i = 361$$

$$\bar{x} = 553/361 = 1.5319$$

$$S = 0.70$$

Table 2

Estimation of survival rate from a single tagging experiment with recaptures on discrete occasions - II

| i | 1 | 2 | 3 | 4 | 5 | 6 |
|---|---|---|---|---|---|---|
| $m_i$ | 120 | 140 | 16 | 35 | 40 | 29 |
| $f_i$ | 10 | 14.5 | 3.2 | 7.9 | 12.3 | 15.8 |
| $y_i$ | 12.00 | 9.66 | 5.00 | 4.43 | 3.25 | 1.84 |

Jackson

$$S = (9.66 + 5.00 + 4.43 + 3.25 + 1.84)/(12.00 + 9.66 + 5.00 + 4.43 + 3.25)$$
$$= 0.70$$

Stevens

$$S = [(5.00 + 4.43 + 3.25 + 1.84)/(12.00 + 9.66 + 5.00 + 4.43)]^{\frac{1}{2}}$$
$$= 0.68$$

Heincke

$$S = (9.66 + 5.00 + 4.43 + 3.25 + 1.84)/(12.00 + 9.66 + 5.00 + 4.43 + 3.25 + 1.84)$$
$$= 0.67$$

Robson and Chapman

$$\Sigma_i(i-1)y_i \; 9.66(1) + 5.00(2) + 4.43(3) + 3.25(4) + 1.84(5) = 55.15$$
$$\Sigma y_i = 36.18$$
$$\bar{x} = 55.15/36.18$$
$$= 1.5243$$
$$S = 0.70$$

Table 3

Estimation of survival rate from a single tagging experiment with continuous recaptures - I

| Months after release | 1-12 | 13-24 | 25-36 | 37-48 |
|---|---|---|---|---|
| Coded period | 1 | 2 | 3 | 4 |
| $m_i$ | 208 | 182 | 156 | 32 |
| $f_i$ | 1.5 | 2.0 | 3.0 | 0.8 |
| $y_i$ | 139 | 91 | 52 | 40 |

Jackson

$S = (91 + 52 + 40)/(139 + 91 + 52) = 0.65$

Stevens

$S = [(52 + 40)/(139 + 91)]^{\frac{1}{2}} = 0.63$

Heincke

$S = (91 + 52 + 40)/(139 + 91 + 52 + 40) = 0.57$

Robson and Chapman

$\Sigma(i-1)\, y_i = 91 + 52(2) + 40(3) = 315$

$\Sigma y_i = 322$

$\bar{x} = 315/322 = 0.9783$

$S = 0.64$

Table 4

Estimation of survival rate from a single tagging experiment with continuous recaptures - II

Regression method of Beverton and Holt (1956)

| Months after release | 1-12 | 13-24 | 25-36 | 37-48 |
|---|---|---|---|---|
| Coded period (i) | 1 | 2 | 3 | 4 |
| Number recaptured per unit effort ($y_i$) | 139 | 91 | 52 | 40 |
| Log ($y_i$) | 4.935 | 4.512 | 3.952 | 3.690 |

Regression of log ($y_i$) on i gives

$\log (y_i) = 5.347 - 0.430i$

Hence $Zp = 0.430$

Hence $Z = 0.430$

$S = \exp - Z = 0.65$

## Table 5

Estimation of survival rate from a single tagging experiment with continuous recaptures - III

Regression method of Gulland (1969)

| Months after release | 1-12 | 13-24 | 25-36 | 37-48 |
|---|---|---|---|---|
| Coded period (i) | 0.5 | 1.5 | 2.5 | 3.5 |
| Number recaptured per unit effort ($y_i$) | 139 | 91 | 52 | 40 |
| Log ($y_i$) | 4.935 | 4.512 | 3.952 | 3.690 |

Regression of log ($y_i$) gives

$$\log (y_i) = 5.132 - 0.430i$$

Hence Zp = 0.430

Hence Z = 0.430

S = exp - Z = 0.65

## Table 6

Estimation of survival rate from a single tagging experiment with continuous recaptures - IV

Weighted regression method of Paulik (1963)

| Months after release | 1-12 | 13-24 | 25-36 | 37-48 |
|---|---|---|---|---|
| Coded period (i) | 1 | 2 | 3 | 4 |
| Numbers recaptured per unit effort ($y_i$) | 139 | 91 | 52 | 40 |
| Log ($y_i/T$) | -1.974 | -2.397 | -2.957 | -3.219 |
| Weighting factor $W_i = y_i/T$ | 0.139 | 0.091 | 0.052 | 0.040 |

T = 1000

Weighted regression of log ($y_i/T$) on i gives

$$\log (y_i/T) = -1.539 - 0.438i$$

Hence Zp = 0.438

Hence Z = 0.438

S = exp -Z

= 0.645

## Table 7

Estimation of survival rate from a single tagging experiment given exact recovery times for each fish recaptured

Number of days absence for individual recaptures

1, 5, 7, 9, 10, 12, 16, 18, 20, 25, 30, 39, 50, 70, 79, 85, 105, 140, 162, 195, 250

Mean duration of freedom $\bar{t}$ = 63 days = 0.17 years

Gulland (1955):

$$Z(\text{annual}) = 1/\bar{t} = \frac{1}{0.17} = 5.9$$

Paulik (1963):

$t = 0.17$

$u = 250/365 = 0.68$ year

$\bar{t}/u = 0.25$

Hence Zu (which is equivalent to $c'x_o$ in Table 1 of Deemer and Votaw, 1955) = 3.55

$\therefore Z = 3.55/0.68 = 5.22$

Table 8

Estimation of survival rate

Jolly-Seber method

| | | Sampling times | | | | | |
|---|---|---|---|---|---|---|---|
| | Numbers tagged ($T_i$) | 2 | 3 | 4 | 5 | 6 | $r_i$ |
| 1 | 1 000 | 60 | 32 | 21 | 13 | 3 | 129 |
| 2 | 2 060 | | 124 | 82 | 49 | 12 | 267 |
| 3 | 1 656 | | | 149 | 89 | 22 | 260 |
| 4 | 1 252 | | | | 188 | 46 | 234 |
| 5 | 2 339 | | | | | 193 | 193 |
| | $m_i$ | 60 | 156 | 252 | 339 | 276 | 1 083 |

Values of q

| 1 | 2 | 3 | 4 | 5 |
|---|---|---|---|---|
| 0 | 69 | 180 | 188 | 83 |

Values of S

$$S\ 1/2 = 129\ [(2060)(69) + (267)(60)]/(267)(1\ 000)(0 + 129)$$
$$= 0.59$$

$$S\ 2/3 = 267\ [(1\ 656)(180) + (260)(156)]/(260)(2\ 060)(69 + 267)$$
$$= 0.50$$

$$S\ 3/4 = 260\ [(1\ 252)(188) + (234)(252)]/(234)(1\ 656)(180 + 260)$$
$$= 0.45$$

$$S\ 4/5 = 234\ [(2\ 339)(83) + (193)(339)]/(193)(1\ 252)(188 + 234)$$
$$= 0.60$$

Table 9

Estimation of survival rate – Robson method

Samples for tagging and recaptures taken during discrete intervals

| | Numbers Tagged ($T_i$) | Sampling times 2 | 3 | 4 | $r_i$ |
|---|---|---|---|---|---|
| 1 | 1 000 | 60 | 36 | 27 | 123 |
| 2 | 2 000 | | 120 | 90 | 210 |
| 3 | 1 500 | | | 135 | 135 |
| | $m_i$ | 60 | 156 | 252 | |

Values of q:

| 1 | 2 | 3 |
|---|---|---|
| 0 | 63 | 117 |

Values of S:

$$S_{1/2} = (2\,000)(63)(123)/(1\,000)(123)(210)$$
$$= 0.60$$

$$S_{2/3} = (1\,500)(117)(210)/(2\,000)(63 + 210)(135)$$
$$= 0.50$$

Table 10

Estimation of survival rate – Robson method

Recaptures made continuously between taggings

| | | Recapture periods | | | | | |
|---|---|---|---|---|---|---|---|
| (i) | Numbers tagged ($T_i$) | 1–2 | 2–3 | 3–4 | 4–5 | 5–6 | $r_i$ |
| 1 | 1 000 | 100 | 72 | 60 | 34 | 12 | 278 |
| 2 | 2 000 | | 240 | 200 | 112 | 40 | 592 |
| 3 | 1 500 | | | 300 | 169 | 61 | 530 |
| 4 | 1 000 | | | | 250 | 90 | 340 |
| 5 | | | | | | 300 | 300 |
| | $m_i$ | 100 | 312 | 560 | 565 | 503 | 2 040 |

Values of q

| 1 | 2 | 3 | 4 | 5 |
|---|---|---|---|---|
| 0 | 178 | 458 | 428 | 203 |

Values of S

$$S\ 1/2 = (2\,000)(178)(278)/[1\,000(0 + 278)592] = 0.60$$

$$S\ 2/3 = (1\,500)(458)(592)/[2\,000(178 + 592)530] = 0.50$$

$$S\ 3/4 = (1\,000)(428)(530)/[1\,500(458 + 530)340] = 0.45$$

$$S\ 4/5 = (2\,000)(203)(340)/[1\,000(428 + 340)300] = 0.60$$

Table 11

Data from Table 9 for application of Bailey's triple catch equation

| Tagging time | Numbers tagged | Recoveries at recapture times 2 | 3 |
|---|---|---|---|
| 1 | 1 000 | 60 | 36 |
| 2 | 2 000 | | 120 |

$T_1 = 1\,000$

$T_2 = 2\,000$

$S_{1/2} = T_2 m_{13} / T_1 m_{23}$

$S_{1/2} = \frac{2\,000(36)}{1\,000(120)} = 0.60$

Table 12

Data from Table 8 for application of Leslie and Chitty's triple catch equation

| Tagging time | Numbers tagged | Recoveries at recapture times 2 | 3 |
|---|---|---|---|
| 1 | 1 000 | 60 | 32 |
| 2 | 2 000 | | 124 |
| | $m_i$ | 60 | 156 |

$T_1 = 1\,000$

$T_2 = 2\,000$

$S_{1/2} = (T_2 m_{13} + m_3 m_{12}) / T_1 m_{23}$

$S_{1/2} = [(2\,000)(32) + (156)(60)] / (1\,000)(124)$

$= 0.59$

Table 13

Estimation of F from data in Tables 4 and 6

From Table 4:

Intercept $I_o$ = 5.347

T = 1 000

$F = 0.430[\exp(5.347 - 0.430)]/1\,000(1-\exp(-0.430))$

$= 0.17$

From Table 6:

Intercept $I_o$ = -1.539

T = 1 000

$F = 0.438[\exp(-1.539-0.438)]/(1-\exp(-0.438))$

$= 0.17$

Table 14

Estimation of F from data in Table 5

Gulland method

Intercept $I_o$ = 5.132

T = 1 000

F = (exp 5.132)/1 000

= 0.17

Table 15

Estimation of F from data in Table 7

T = 1 000

m = 21

$\bar{t}$ = 0.17 years

Gulland's method:

F = 21/1 000 (0.17)

= 0.12

X = Z - F = 5.9 - 0.12 = 5.78

Chapman's method:

F = 20/1 000 (0.17)

= 0.12

Table 16

A: Estimation of the rate of capture (p) using the data in Table 8

| | Basic data | | | | Estimated values | |
|---|---|---|---|---|---|---|
| | $T_i$ | $q_i$ | $r_i$ | $m_i$ | $I_i$ | $p_i$ |
| 1 | 1 000 | 0 | 129 | - | - | - |
| 2 | 2 060 | 69 | 267 | 60 | 592 | 0.10 |
| 3 | 1 656 | 180 | 260 | 156 | 1 302 | 0.12 |
| 4 | 1 252 | 188 | 234 | 252 | 1 258 | 0.20 |
| 5 | 2 339 | 83 | 193 | 339 | 1 345 | 0.25 |

B: Estimation of the rate of capture (p) using the data in Table 9

| | Basic data | | | | Estimated values | |
|---|---|---|---|---|---|---|
| | $T_i$ | $q_i$ | $r_i$ | $m_i$ | $I'_3$ | $p_i$ |
| 1 | 1 000 | 0 | 123 | 0 | 0 | - |
| 2 | 2 000 | 63 | 210 | 60 | 600 | 0.10 |
| 3 | 1 500 | 117 | 135 | 156 | 1 300 | 0.12 |

$I_i' = I_i = T_i q_i / r_i$

$p_i = m_i / I_i$

Table 17

Estimation of F using the data in Table 10

| i | $T_i$ | $q_i$ | $r_i$ | $m_i$ | $S_i$ | $Z_i$ | $N_i$ | $F_i$ |
|---|---|---|---|---|---|---|---|---|
| 1 | 1 000 | 0 | 278 | 100 | 0.60 | 0.51 | 1 000 | 0.13 |
| 2 | 2 000 | 178 | 592 | 312 | 0.50 | 0.69 | 2 601 | 0.17 |
| 3 | 1 500 | 458 | 530 | 560 | 0.45 | 0.80 | 2 796 | 0.29 |
| 4 | 1 000 | 428 | 340 | 565 | 0.60 | 0.51 | 2 559 | 0.28 |

$N_i = T_i (q_i + r_i)/r_i$

$F = Zm/N(1 - S)$

Table 18

Formulae for estimating population size (N) by the Petersen method

| Reference | Type of Sampling | Estimates of | |
|---|---|---|---|
| | | Population size (N) | Variance of (N) |
| A. Bailey, 1951 | Direct | $N = \frac{Tn}{m}$ | $\text{var } N = \frac{T^2 n(n-m)}{m^3}$ |
| B. Bailey, 1951 | Direct | $N = \frac{T(n+1)}{m+1}$ | $\text{var } N = \frac{T^2(n+1)(n-m)}{(m+1)^2(m+2)}$ |
| C. Chapman, 1951<br>Schaefer, 1951 | Direct | $N = \frac{(T+1)(n+1)}{m+1} - 1$ | $\text{var } N = N^2\left(\frac{N}{nT} + 2\left(\frac{N}{nT}\right)^2 + 6\left(\frac{N}{nT}\right)^3\right)$ |
| D. (Bailey, 1951)<br>(Chapman, 1952) | Inverse | $N = \frac{n(T+1)}{m} - 1$ | $\text{var } N = \frac{(T-m+1)(N+1)(N-T)}{m(T+2)}$ |

Table 19

Estimation of population size by the Jolly and Seber method

| i | $I_i$ | $m_i$ | $n_i$ | $N_i$ |
|---|---|---|---|---|
| 1 | - | - | - | - |
| 2 | 592 | 60 | 16 000 | 158 000 |
| 3 | 1 302 | 156 | 10 000 | 84 000 |
| 4 | 1 258 | 252 | 7 000 | 35 000 |
| 5 | 1 345 | 339 | 5 500 | 22 000 |

Values of $I_i$ and $m_i$ from Table 16A

Values of $n_i$ supplied for purposes of the example

$N_i = n_i I_i / m_i$

Table 20

Example of the estimation of growth parameters from tagging data

| a | Lt | $L_{t+a}$ | y | x | $b_1$ | | |
|---|---|---|---|---|---|---|---|
| Time of liberty (years) | Length at release (cm) | Length at recapture (cm) | $\frac{L_{t+a} - Lt}{a}$ | $\frac{L_{t+a} + Lt}{2}$ | $\frac{1}{2}K_1 a$ | $\frac{b_1}{\tanh b_1}$ | $y \cdot \frac{b_1}{\tanh b_1}$ |
| 0.5 | 9.1 | 16.9 | 15.6 | 13 | 0.05 | 1.0008 | 15.6 |
| 0.8 | 24.2 | 33.8 | 12.0 | 29 | 0.08 | 1.0021 | 12.0 |
| 1.0 | 41.5 | 50.5 | 9.0 | 46 | 0.10 | 1.0033 | 9.0 |
| 0.4 | 61.9 | 64.1 | 5.5 | 63 | 0.04 | 1.0005 | 5.5 |
| 1.2 | 74.2 | 77.8 | 3.0 | 76 | 0.12 | 1.0048 | 3.0 |

Table 21

Example of the calculation of movement parameters from tagging data

| $r_i$(km) | $\theta^o_i$ | $t_i$(days) | sin $\theta_i$ | cos $\theta_i$ | $r_i \sin \theta_i$ | $r_i \cos \theta_i$ | $r_i^2/t_i$ |
|---|---|---|---|---|---|---|---|
| 5 | 58 | 18 | +.848 | +.530 | + 4.24 | + 2.65 | 1.4 |
| 50 | 150 | 60 | +.500 | -.866 | +25.00 | -43.30 | 41.7 |
| 20 | 230 | 30 | -.766 | -.643 | -15.32 | -12.86 | 13.3 |
| 30 | 335 | 45 | -.423 | +.906 | -12.69 | +27.18 | 20.0 |
| Totals | | 153 | | | + 1.23 | -26.33 | 76.4 |

$R = \sqrt{1.23^2 + (-26.33)^2} = 26.36$

$V = 26.36/153 = 0.17$ km/day

$a^2 = \frac{1}{4}\{76.4 - \frac{694.8}{153}\} = 18$ km$^2$/day

Table 22

Showing some possible combinations of values of $\epsilon$ and v such that $\epsilon.v = 4.0$ km$^2$/day

| (km) $\epsilon$ | v (km/day) |
|---|---|
| 4 | 1 |
| 1 | 4 |
| 0.1 | 40 |
| 0.01 | 400 |

Figure 1

Showing a way of classifying tag returns

Sampling Times

| 2 | 3 | 4 | 5 | 6 | 7 | Total recaptures |
|---|---|---|---|---|---|---|
| $m_{12}$ | $m_{13}$ | $m_{14}$ | $m_{15}$ | $m_{16}$ | $m_{17}$ | $r_1$ |
| | $m_{23}$ | $m_{24}$ | $m_{25}$ | $m_{26}$ | $m_{27}$ | $r_2$ |
| | | $m_{34}$ | $m_{35}$ | $m_{36}$ | $m_{37}$ | $r_3$ |
| | | | $m_{45}$ | $m_{46}$ | $m_{47}$ | $r_4$ |
| | | | | $m_{56}$ | $m_{57}$ | $r_5$ |
| | | | | | $m_{67}$ | $r_6$ |

Total recaptures:

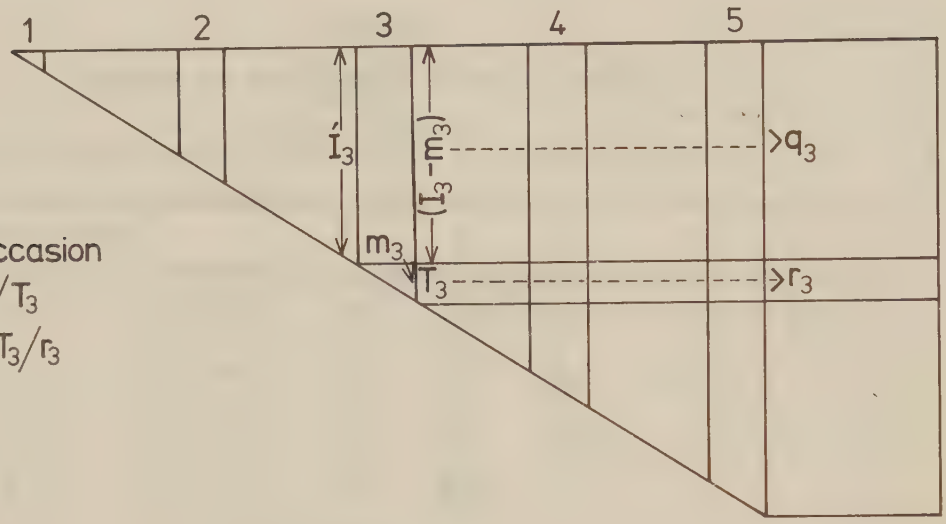
$m_2$ $m_3$ $m_4$ $m_5$ $m_6$ $m_7$

$m_{ij}$ = number liberated on the ith sampling occasion and recaptured on the jth sampling occasion;

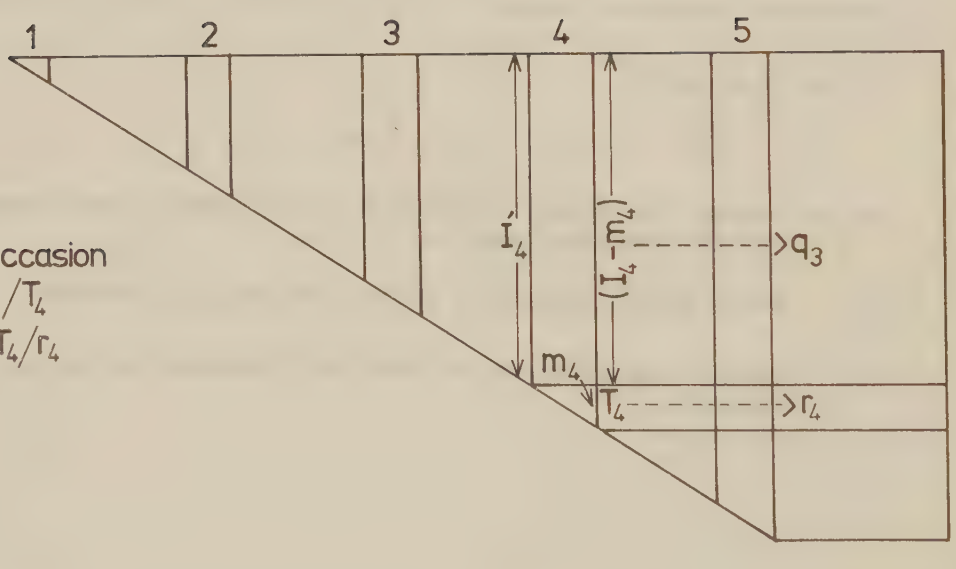
$m_j$ = total number recaptured on the jth sampling occasion;

$r_i$ = number recaptured out of the fish liberated on the ith sampling occasion.

# Fig. 2 ESTIMATION OF SURVIVAL RATE
## Method of Jolly and Seber




For the 3rd occasion
$q_3/(I_3-m_3) = r_3/T_3$
$\therefore I_3 = m_3 + q_3 T_3/r_3$




For the 4th occasion
$q_4/(I_4 - m_4) = r_4/T_4$
$\therefore I_4 = m_4 + q_4\ T_4/r_4$

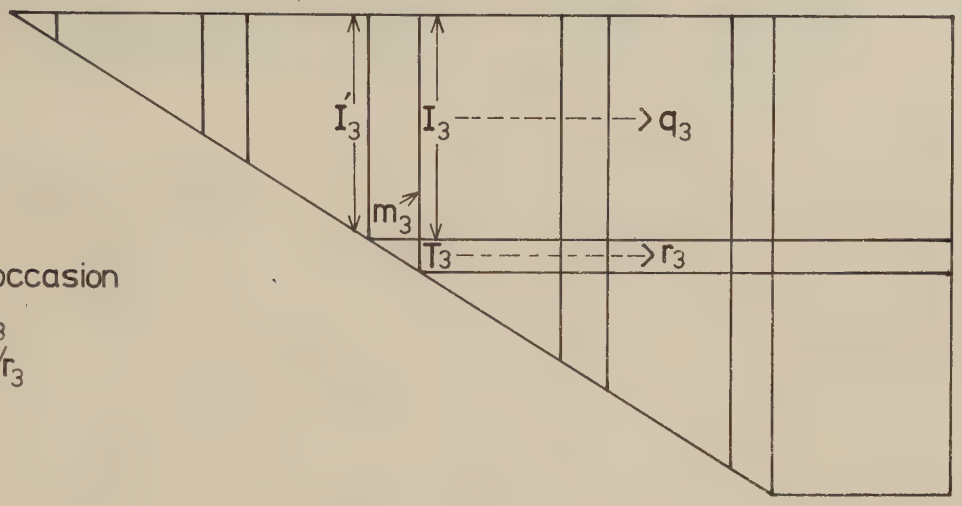
The proportion surviving from the end of the 3rd to the end of the 4th occasion is given by:

$$S_{3/4} = I_4/(I_3 - m_3 + T_3) = \frac{r_3(T_4\ q_4 + r_4\ m_4)}{r_4\ T_3(q_3 + r_3)}$$

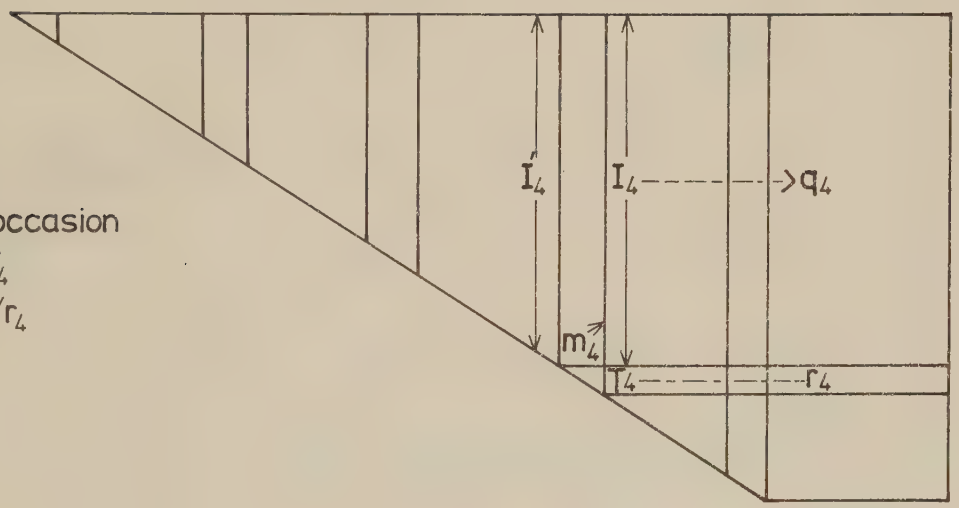
In general

$$S_{t/t+1} = \frac{r_t\ (T_{t+1}\ q_{t+1} + r_{t+1}\ m_{t+1}\ )}{r_{t+1}\ T_t(q_t + r_t\ )}$$

# Fig. 3 ESTIMATION OF SURVIVAL RATE Method of Robson




For the 3rd occasion
$q_3 / I_3 = r_3 / T_3$
$\therefore I_3 = T_3\, q_3 / r_3$




For the 4th occasion
$q_4 / I_4 = r_4 / T_4$
$\therefore I_4 = T_4\, q_4 / r_4$

The proportion surviving from the end of the 3rd to the end of the 4th occasion is given by:

$$S_{3/4} = I_4/(I_3 + T_3) = \frac{T_4\, q_4\, r_3}{T_3\, r_4 (q_3 + r_3)}$$

In general

$$S_{t/t+1} = \frac{T_{t+1}\, q_{t+1}\, r_t}{T_t\, r_{t+1}\, (q_t + r_t)}$$

# Fig. 4 ERRORS OF TYPES A, B & C

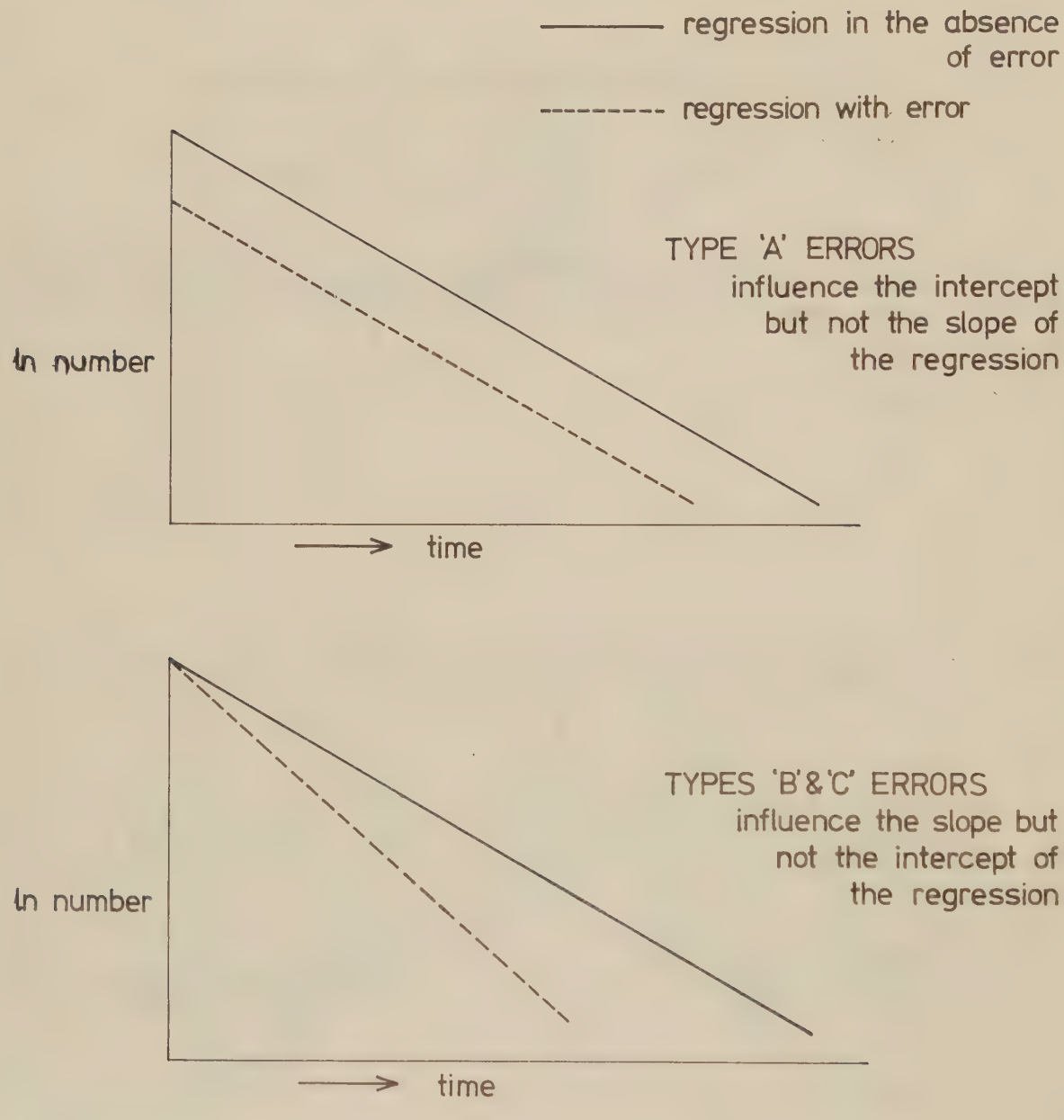

regression in the absence of error
regression with error
TYPE 'A' ERRORS
influence the intercept but not the slope of the regression
ln number
time
TYPES 'B' & 'C' ERRORS
influence the slope but not the intercept of the regression
ln number
time

Fig. 5 SHOWING THE RELATIONSHIP BETWEEN THE POSITIONS OF LIBERATION (A) AND RECAPTURE (B) OF A FISH WITH REFERENCE TO THE CO ORDINATE SYSTEM NESW

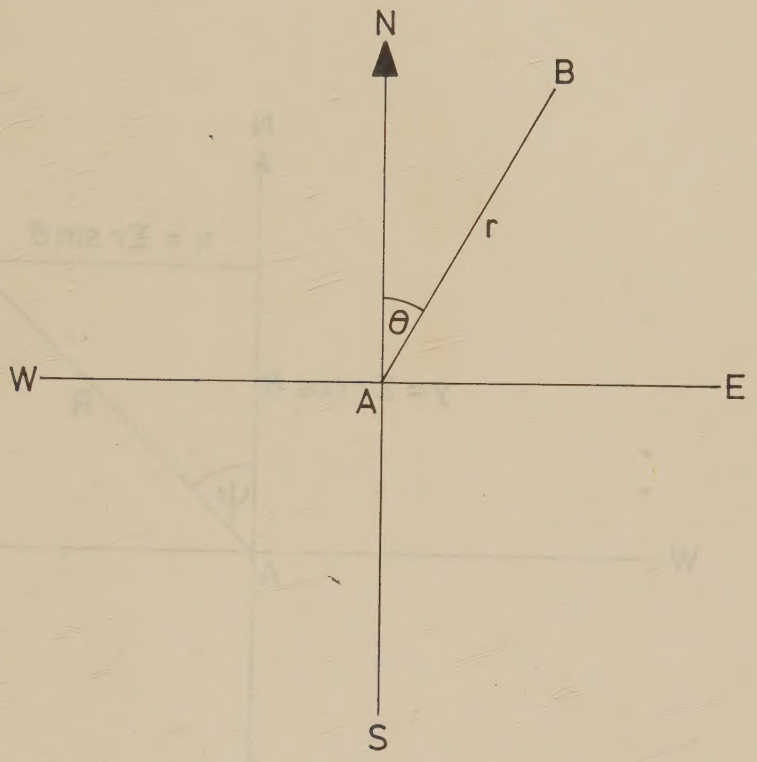



Fig. 6

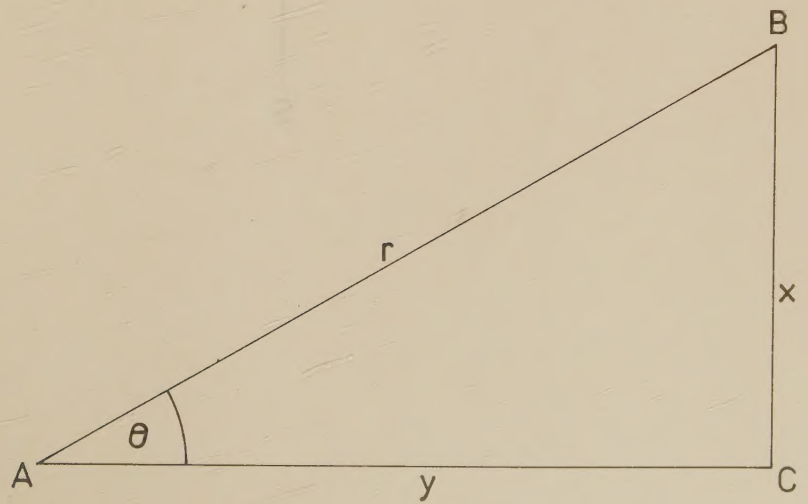
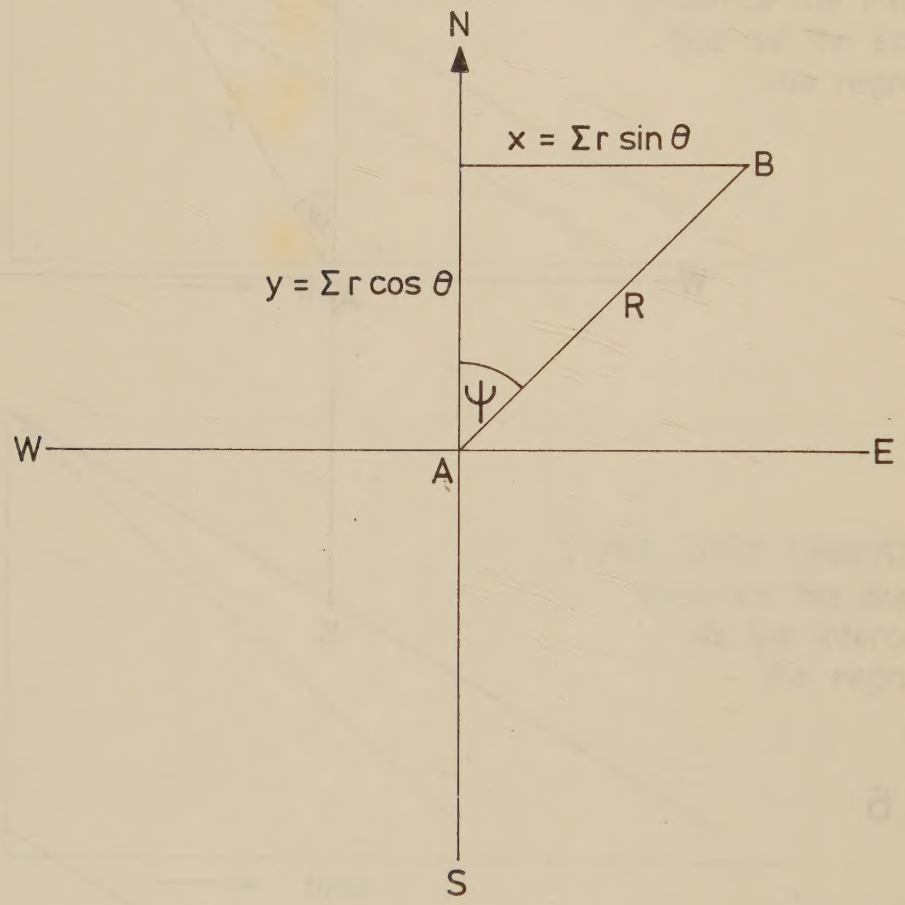


Fig. 7 DETERMINATION OF THE OVERALL GROUP DISPLACEMENT, R



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ISBN 92-5-100051-4